

Dentition of etmopterid shark *Miroscyllium* (Squaliformes) with comments on the fossil record of lanternsharks

by

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ABSTRACT. - Although modern lantern sharks (Etmopteridae, Squaliformes) are taxonomically diverse, their phylogenetic relationships remain unclear. Numerous fossil etmopterids have been recently discovered, and their geologic occurrences are reviewed here. The dentition of the rare recent etmopterid *Miroscyllium sheikoi* is described. The species shows peculiar ontogenetic changes in the morphology of lower and upper teeth, and allows to assign some fossil material described as *Centroscyllium* by Ledoux (1972) to *Miroscyllium*. Moreover, the presence, in *Miroscyllium sheikoi*, of a morphological transitional dental type between *Etmopterus* and *Centroscyllium*, and its discovery in the fossil record allow to propose an alternative way to contribute to the phylogenetic frameworks.

RÉSUMÉ. - À propos de la dentition de *Miroscyllium* (Squaliformes) et commentaires sur les requins lanternes fossiles.

Bien que le groupe des requins lanternes (Etmopteridae, Squaliformes) soit actuellement bien diversifié, leur histoire et les relations phylogénétiques au sein de cette famille restent encore obscures. Plusieurs fossiles d'Etmopteridae ont été décrits ces 15 dernières années et une courte synthèse de ces descriptions est présentée ici afin de mieux comprendre leur histoire évolutive et leur diversification. L'observation détaillée de la dentition de plusieurs individus de l'unique espèce actuelle du genre *Miroscyllium*, *M. sheikoi*, a permis de montrer un changement ontogénique très particulier de la denture. Cette observation a permis de réattribuer quelques fossiles décrits en 1972 par Ledoux au genre *Miroscyllium* et non au genre proche *Centroscyllium*. Ainsi la présence, au cours du développement de *M. sheikoi*, d'une transition morphologique entre la denture du genre *Centroscyllium* et celle du genre *Etmopterus*, ajoutée à la découverte de représentants fossiles du genre *Miroscyllium*, permet de proposer une approche alternative pour la compréhension des relations phylogénétiques au sein des Etmopteridae.

Key words. - Etmopteridae - *Miroscyllium* - Tooth morphology - Ontogenetic change - Palaeontology - Evolution.

The family Etmopteridae Fowler, 1934 includes actually five genera and possibly up to 44 species (Compagno, 1999, 2005; Last *et al.*, 2002). The Etmopteridae display a latitudinal distribution between 60°N and 50°S (Compagno, 1984; personal database). They have benthic or neritic habits with a wide bathymetric range (from 0 to 2850 m depth), even if most species of this family live between 300 and 700 m depth. Available biological information is still limited for almost all etmopterid species, and many species remain to be described.

Phylogenetic relationships within the family have remained unclear for a long time. The monophyly of Etmopteridae and the phylogenetic relationships within the group are based on general anatomy and particularity of luminous organs (Shirai and Nakaya, 1990a, 1990b; Shirai, 1996). According to Shirai (1992), *Etmopterus* and *Miroscyllium* are considered as the basal taxa of the family and appear to be the sister group of *Aculeola*, *Centroscyllium* and *Trigonognathus*. However Adnet and Cappetta (2001) reexamined

the phylogenetics based on the same data (performed with PAUP 3.11 software: Swofford, 1993) and are not in agreement with Shirai's (1992) conclusions. Shirai's (1992) phylogenetic reconstruction does not allow to distinguish distinct groups within the monophyletic family. Carvalho and Maisey (1996) checked Shirai's (1992) analysis, computing a new database and obtaining different results. According to them, *Trigonognathus* appears to be the most primitive taxon and the *Etmopterus-Miroscyllium* clade is sister to the *Aculeola-Centroscyllium* clade. Phylogenetic analysis based on dental morphology of living and fossil Squaliformes does not allow to solve this problem (Adnet and Cappetta, 2001). In fact, the family Etmopteridae exhibits one of the largest diversity in dental morphology among elasmobranchs. According to the criteria defined by Cappetta (1986, 1987), three dental types can be observed in the living etmopterid species: tearing (Fig. 1A; one species), grasping (Fig. 1B; nine species), and cutting-grasping (Fig. 1C; 31 to 35 species).

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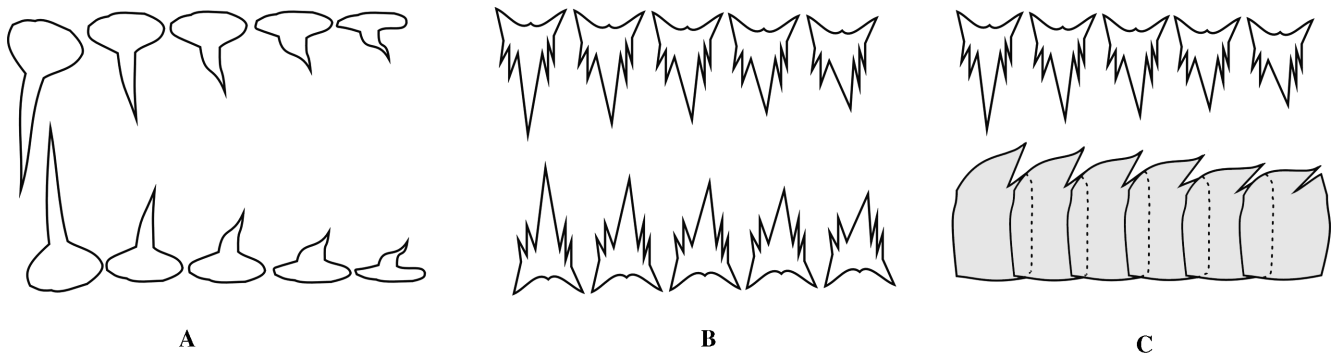


Figure 1. - Dental types in Etmopteridae. **A:** Tearing-type (e. g., *Trigonognathus*); **B:** Clutching-type (*Centroscyllium*, *Aculeola*, and adult *Miroscyllium*); **C:** Cutting-clutching subtype (*Etmopterus* and juvenile *Miroscyllium*). [Différentes formes de dents chez les Etmopteridae. **A** : Type arracheur (chez *Trigonognathus*); **B** : Type agrippeur (chez *Centroscyllium*, *Aculeola* et les individus adultes de *Miroscyllium*) ; **C** : Sous-type agrippeur-coupeur (chez *Etmopterus* et les individus juvéniles de *Miroscyllium*).]

Recent phylogenetic classifications of Etmopteridae remain unclear but new studies based on molecular analysis of living species is anticipated to elucidate the phylogenetic relationships of lantern sharks. However, we can now explore one aspect of lantern shark evolutionary history in the light of their fossils representatives. The purpose of the present work is to update our knowledge of the fossil record of Etmopteridae and to reconstruct their evolutionary patterns.

Fossil sharks are mostly known from isolated teeth. Therefore, observations on the dentitions of living species become essential for palaeontologists. In addition to the direct observation of recent material, accurate illustrations of the living Etmopteridae dentitions are available in recent literature (Herman *et al.*, 1989; Cappetta and Adnet, 2001). Because of the scarcity of available specimens, the dentition of the genus *Miroscyllium* was very poorly known until now. In this study, we examined the dentition of some recent specimens of *Miroscyllium sheikoi* (Rasptooth dogfish) in detail for the first time using scanning electron microscope images. In the light of new observations of *M. sheikoi*, new attributions of fossil material are possible.

THE DENTITION OF THE RECENT *MIROSCYLLIUM*

Previously described as *Centroscyllium sheikoi*, Shirai and Nakaya, (1990b) established a new genus, *Miroscyllium*, based on three adult and young male specimens fished off Kyushu-Palau ridge, housed in the collections of the Laboratory of Marine Zoology, Hokkaido University, Faculty of Fisheries, Hakodate, Japan (HUMZ). The first illustration of teeth (Shirai and Nakaya 1990b: fig. 4, p. 351) of the only species *M. sheikoi* allowed a limited comparison of its dental morphology with other living Etmopteridae. According to Shirai and Nakaya (1990b), the lower dentition of *M. sheikoi*

displays a strong ontogenetic heterodonty. It is characterised by weak or lack of overlapping of dental files and the passage to a multicuspidate crown in adult specimens (character 9, p. 351). The juvenile dental morphology is close to *Etmopterus* species (overlapping of lower files and monocuspidate crown in the lower tooth). The dentition of two recent specimens, a juvenile and an adult, of the living species *M. sheikoi* was examined. Teeth were extracted by dissection and examined with a scanning electron microscope. Despite the preservative used to fix the specimens, which altered tooth enameloid, the examination offered an opportunity to document its peculiar dental characters in this genus (Fig. 2).

ADULT *MIROSCYLLIUM SHEIKOI* (42.5 cm TL male, HUMZ 74978: Fig. 2A-H)

Upper teeth (Fig. 2A-D)

The morphology of upper teeth is close to those of some *Etmopterus* species. The crown is symmetrical or slightly asymmetrical and shows a fine and slender median cusp with two to three pairs of high and sharp lateral cusplets on each side. The root is clearly bilobate. The labial face of the root shows some small lateral nutritive foramina and the medio-lingual nutritive foramen opens close the crown-root boundary on the lingual protuberance. The intra-individual morphological variations seem to be not important, but it was not possible to observe clearly the very lateral files because it was not possible to open completely the mouth of the specimen without damaging it.

Lower teeth (Fig. 2E-H)

The lower teeth (Fig. 2E, F), including lateral teeth (Fig. 2G, H), are rather tall with a median cusp and two pairs of lateral cusplets. The cusplets close to the main cusp are very high, while the external ones are much shorter. The root

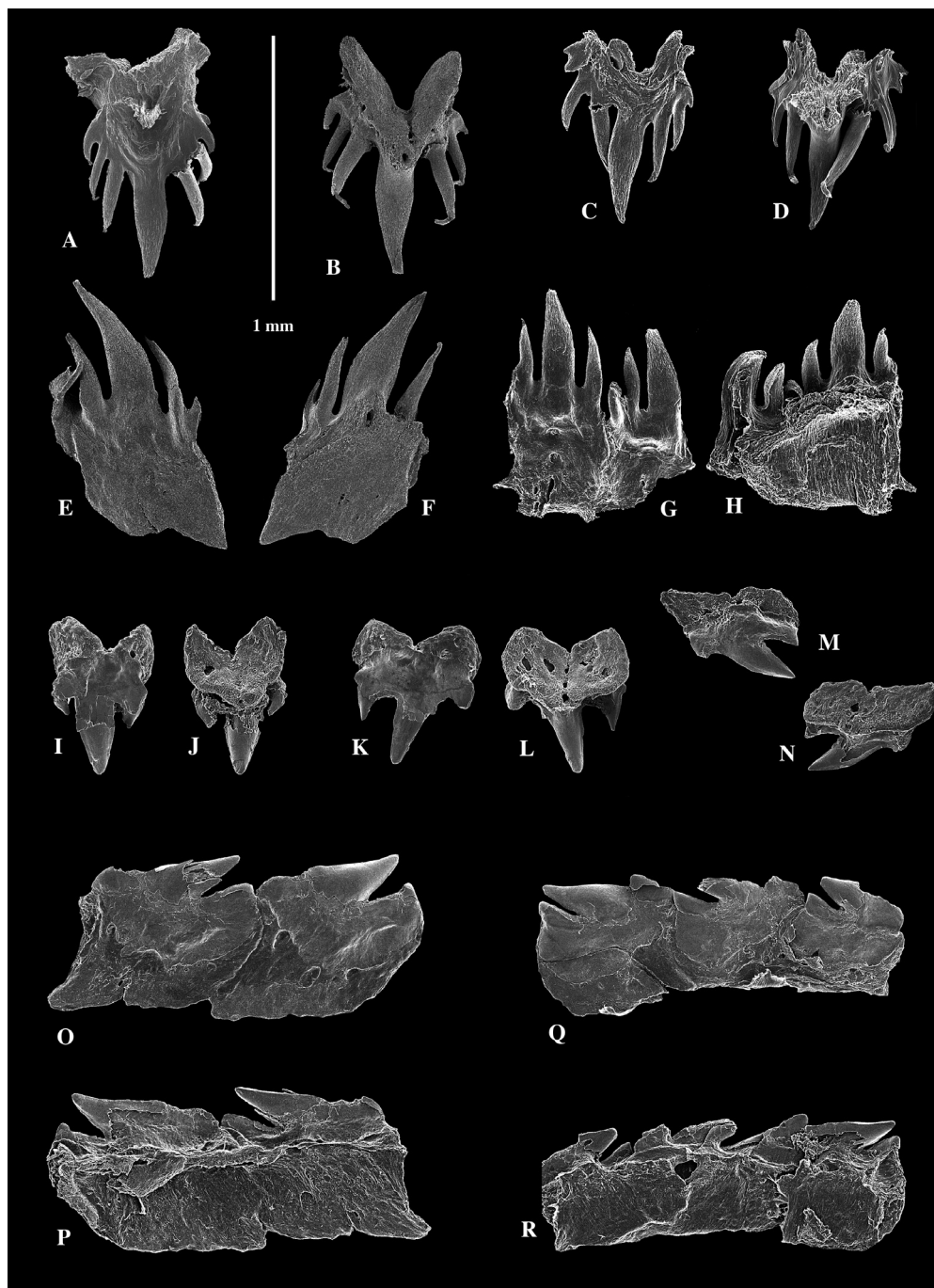


Figure 2. - Teeth of adult (A-H, HUMZ 74978) and juvenile (I-R, HUMZ 74984) male specimens of Recent *Miroscyllium sheikoi*. **A**: Upper anterior tooth, labial view; **B**: Upper anterior tooth, lingual view; **C**: Upper anterolateral tooth, labial view; **D**: Same specimen, lingual view; **E**: Lower anterior tooth, labial view; **F**: Lower anterior tooth, lingual view; **G**: Lower anterolateral teeth, labial view; **H**: Lower lateral teeth, lingual view. **I**: Upper anterior tooth, labial view; **J**: Upper anterior tooth, lingual view; **K**: Upper anterolateral tooth, labial view; **L**: Same specimen, lingual view; **M**: Upper lateral tooth, labial view; **N**: Same specimen, lingual view; **O**: Lower anterolateral teeth, labial view; **P**: Same specimen, lingual view; **Q**: Lower lateral teeth, labial view; **R**: Same specimen, lingual view. [Dents des individus mâles adultes (A-H) et juvéniles (I-R) de *Myroscyllium sheikoi*. **A** : Dent antérieure supérieure, vue labiale ; **B** : Dent antérieure supérieure, vue linguale ; **C** : Dent latéro-antérieure supérieure, vue labiale ; **D** : Même spécimen, vue linguale ; **E** : Dent antérieure inférieure, vue labiale ; **F** : Dent antérieure inférieure, vue linguale ; **G** : Dents latéro-antérieures inférieures, vue labiale ; **H** : Dents latérales inférieures, vue linguale ; **I** : Dent antérieure supérieure, vue labiale ; **J** : Dent latérale supérieure, vue labiale ; **K** : Dent latéro-antérieure supérieure, vue labiale ; **L** : Même spécimen, vue linguale ; **M** : Dent latérale supérieure, vue labiale ; **N** : Même spécimen, vue linguale ; **O** : Dent latéro-antérieure, vue labiale ; **P** : Même spécimen, vue linguale ; **Q** : Dents latérales inférieures, vue labiale ; **R** : Même spécimen, vue linguale.]

is taller than broad, and is flat and parallelepipedic. The basal face is well developed with a mediolingual foramen opening close to the crown-root boundary.

JUVENILE *MIROSCYLLIUM SHEIKOI*
(21.0 cm TL, male, HUMZ 74984: Fig. 2I-R)

Upper teeth (Fig. 2I-N)

The anterior teeth (Fig. 2I, J) show a triangular and labiolingually flattened main cusp with a pair of rather broad and short lateral cusplets. The root is bilobate with rather wide lobes. The basal face is very flat. A second pair of small lateral cusplets might be present in anterolateral files. In more distal files (Fig. 2K, L), the teeth are broader. The cusp slightly inclines distally, with a low and broad mesial cusplet and a sharper distal one well separated from the main cusp. In lingual (and labial) view, the basal edge of the root is medially angular and the basal face is broad with a series of foramina medially aligned. In lateral files (Fig. 2M, N), the teeth are very asymmetrical with a main cusp that is strongly bent distally, a mesial cusplet that is very low, and a distal one that is reduced to an oblique heel. The root shows a parallelepipedic outline with a well marked central foramen on the lingual face.

Lower teeth (Fig. 2O-R)

The lower teeth are rather similar to those of *Etmopterus*. The cusp is narrow, strongly bent distally, and separated from a high, oblique distal heel by a deep notch. The root is well developed but it is difficult to observe the details clearly, particularly the labial enamel-root boundary or the foramina, because of the imperfect state of preservation of the material.

On both specimens, it was not possible to observe the complete dentition, and therefore, to have the total tooth count because of their preservation; the complete opening of the mouth would have seriously damaged them. Even if not all the ontogenetic states are available, it is possible to observe the presence of common characters with lower teeth of *Etmopterus* species such as a strongly labiolingually flattened subrectangular root, some weak mesial and distal overlapping surfaces often restricted to the mesial and distal edges of the root, and a mediolingual foramen below the crown-root boundary. Apart from the last characters, lower teeth of adult *M. sheikoi* show many unique characters such as a multicuspidate crown with two or three pairs of sharp lateral cusplets on each side of the main cusp, an undifferentiated lingual and basal face, a small apron which may be absent, a reduction or absence of marginolabial nutritive foramina, and a mediobasal nutritive foramen that is strongly reduced.

The genus *Miroscyllium* can be distinguished from *Acu-leola*, *Centrosyllium*, and *Trigonognathus* by the occurrence of multicuspidate and strongly labiolingually flattened teeth, at least for the lower teeth of adult specimens. On the basis of dental morphology, there is no doubt that this genus is phylogenetically close to the genus *Etmopterus*. Teeth of *Miroscyllium*, however, differ from those of *Etmopterus* by the occurrence of a multicuspidate crown and more widely spaced files in lower teeth of adult specimens.

FOSSIL LANTERN SHARKS

Fossil remains of living etmopterids taxa are very rare. Because most of the living etmopterids are deep-water sharks, stratigraphic gaps in the fossil record can be explained by the scarcity of deep-water fossiliferous deposits accessible to study. Three fossil etmopterid species are known to date: *Etmopterus bonapartei* from the Zanclean of Italy, *Etmopterus acutidens* from the Eocene-Oligocene of West Indies, and *Trigonognathus virginiae* Cappetta & Adnet, 2001 from the Lutetian of southwestern France. Moreover, in regard to Casier's illustrations, *E. acutidens* was described on the basis of fragmentary lower and upper teeth, which are similar to other contemporary fossil species of Squaliformes, such as *Squaliolus schaubi*. Some other fossil taxa could also belong to the genus *Etmopterus*, such as specimens from the Middle Eocene of Landes, southwestern France (Adnet, 2000), from the Burdigalian-Langhian of Vaucluse, south of France (Ledoux, 1972), from Tortonian of San Agatha Fossili, Italy (Cappetta, unpubl.), from the Lower Miocene of Bavaria (Barthelt *et al.*, 1991, not figured), and from the Zanclean of Italy (Cigala Fulgosi, 1986). However, only one fossil taxon is morphologically close to another genus, *Centrosyllium* from the Burdigalian-Langhian of Vaucluse (Ledoux, 1972). As described below, this material in fact must be placed in the genus *Miroscyllium*.

Fossil etmopterid taxa without living descendants are curiously more diversified and better known. Three different monospecific genera are recognized in northern Europe. The fossil genus *Eoetmopterus* Müller and Schöllmann, 1989 (Upper Campanian of Germany) possibly emerged as early as the Cenomanian (Underwood and Mitchell, 1999), but more likely in the lower Campanian (Thies and Müller, 1993) and became extinct in the Maastrichtian (Herman, 1982; Siverson, 1993). The genus *Proetmopterus* Siverson, 1993 occurs from the Campanian to the Maastrichtian (Herman 1982; Müller and Schöllmann, 1989; Siverson, 1993; Siverson and Cappetta, 2001) and *Microetmopterus* Siverson, 1993 is limited to the Maastrichtian of Sweden.

According to Siverson (1993), the abundance of these fossil etmopterids in the Cretaceous Period can be explained by the shallow-water environment of fossil taxa in contrast

to the deep-water distribution of recent etmopterids. The close phylogenetic relationships of these Cretaceous etmopterids with living taxa remain uncertain and appear to be more complex than implied in a recent phylogenetic analysis of Squaliformes based on dental characters (Adnet and Capetta, 2001). The origin of recent Etmopteridae is not clearly understood presently.

MIROSCYLLIUM SP.

(Fig. 3)

Materials

Two teeth originally described by Ledoux (1972, fig. 10, p. 157) as *?Centrosyllium* sp. from the Lower Langhian (Middle Miocene) of Bonpas (Vaucluse, southern France) are assigned here to *Miroscyllium*, by comparison with the recent species *M. sheikoi*.

Description

The largest tooth, 1 mm wide (Fig. 3A, B), is a lower tooth probably from an anteriolateral file. The crown is broader than high and has a slender and slightly distally crooked main cusp that shows a concave mesial cutting-edge and a slightly convex distal cutting-edge. The main cusp is accompanied by three sharp secondary cusps, two of which (broken) are located on the mesial and one on the distal heel. The height of the distal secondary cusp reaches the lower half of the main cusp. The labiodistal extremity of the crown shows a clear and high convexity at the level of the articular surface (Fig. 3A). The root is broader than its height and is strongly labiolingually compressed. It possesses a flat labial face pitted with irregular elliptical foramina at the level of the enameloid-root junction in which the one below the main cusp is the largest. The labiomesial articular facet is well-marked and occupies the complete height of the labial face. The basal face is flat and occupies almost all the height and the width of the root.

The linguodistal articular facet is as high and deep as the basal face (Fig. 3B). The lingual face is limited to the transversal bulge that appears in relief in comparison with the crown. The small mediolingual foramen opens on the transverse bulge whereas the mediobasal foramen and a superficial groove are placed on the median part of the basal face.

The other tooth (Fig. 3C, D) is very small and comes either from a more lateral file or from a younger individual. Compared with the larger one, this tooth shows a monocuspidate crown very similar to the crown of the species of *Etmopterus* (Herman *et al.*, 1989). The cusp is long and distally crooked but does not overhang the distal extremity of the crown in labial or lingual view. The heel is well-developed and convex. The root, broader than high, shows a small labial face, and the enameloid extends downwards on the root for a rather long distance. The marginolabial foramina are less numerous and proportionally broader. The articular facets (Fig. 3D) are as developed as on the large tooth and the mediobasal foramen opens slightly higher on the basal face.

DISCUSSION

In *Miroscyllium*, the occurrence of a rectangular and labiolingually flattened root, mesially and distally well-marked articular facets throughout the root height, a flat labial face and a lingual face restricted to the transversal bulge, as well as a secondary mediobasal foramen, is similar to the condition found in *Etmopterus*. As for the recent *M. sheikoi*, the fossil *Miroscyllium* sp. can be distinguished by teeth with a multicuspidate crown in adult specimens. Fossil *Miroscyllium* is separated from the recent *M. sheikoi* by a less derived state of a cusp that is distally crooked and with a concave mesial cutting edge, a still clear individualization of the crown in comparison with the root, many marginolabial foramina, a still clearly individualized lingual face by the transversal bulge, and well-developed articular facets.

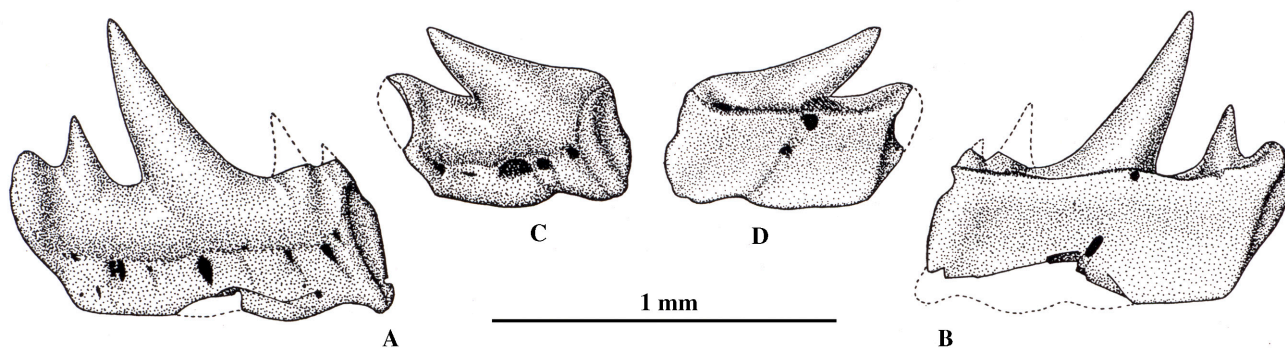


Figure 3. - Fossil teeth of *Miroscyllium* sp. (Ledoux collection; Langhian, level 1, of Bonpas, Vaucluse, southern France), **A**: Lower antero-lateral tooth, labial view; **B**: Same specimen, lingual view; **C**: Lower lateral tooth, labial view; **D**: Same specimen, lingual view. [*Dents fossiles de Miroscyllium* sp. (Collection Ledoux ; Langhien, niveau 1 de Bonpas, Vaucluse, Sud de la France), **A** : Dent latéro-antérieure inférieure, vue labiale ; **B** : Même spécimen, vue linguale ; **C** : Dent latérale inférieure, vue labiale ; **D** : Même spécimen, vue linguale.]

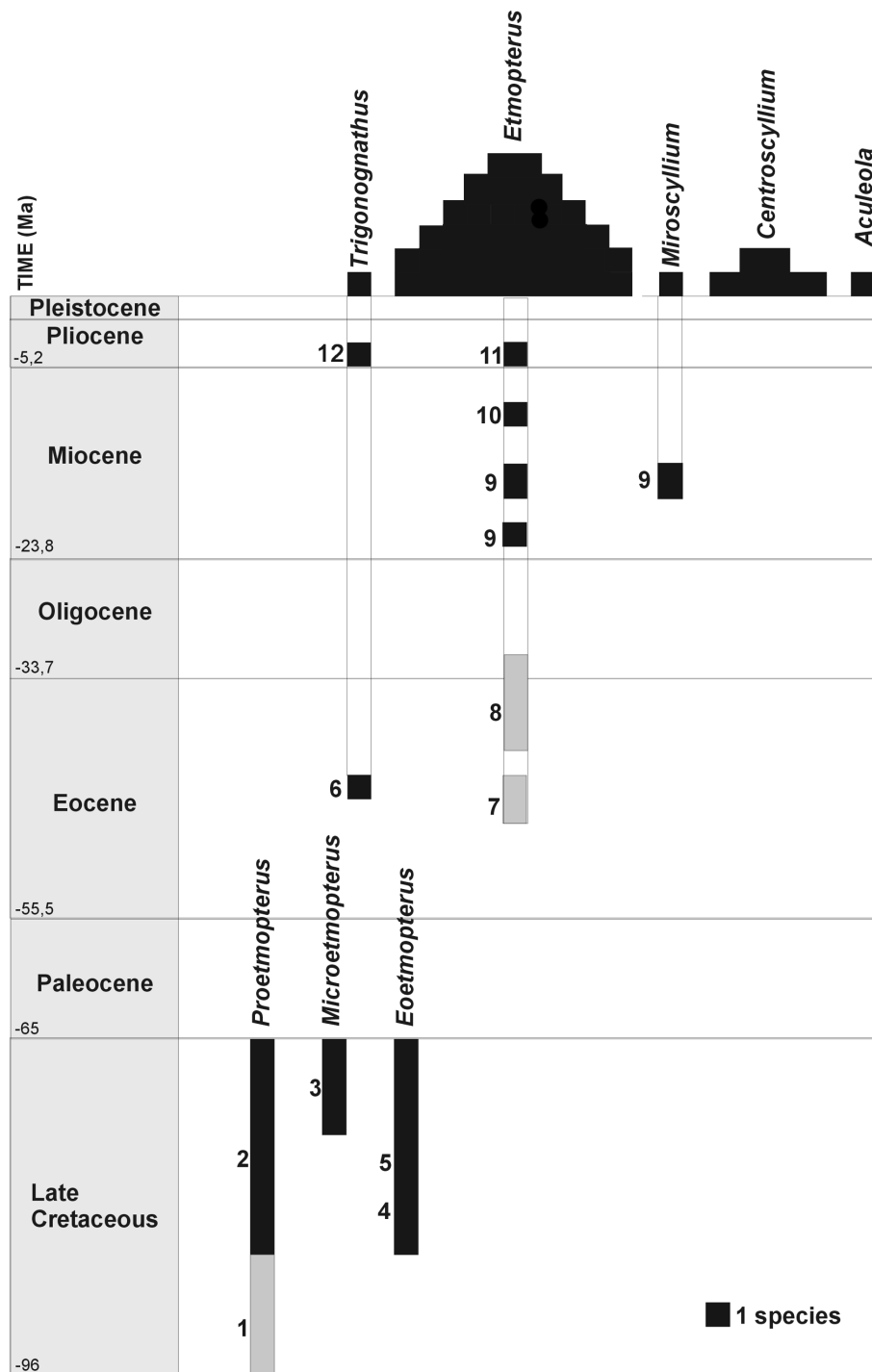


Figure 4. - Fossil record of etmopterid genera. Black boxes indicates the presence of etmopterid taxa and grey boxes, the probable occurrence of fossil species. Diversity in term of number of species is represented by abundance of boxes. References noted near corresponding boxes. 1: Underwood and Mitchell (1999); 2 and 3: see Siverson (1993), Siverson and Cappetta (2001); 4: Siverson (1993), Thies and Müller (1993); 5: modified from Welton and Farish (1993); 6: Cappetta and Adnet (2001); 7: Adnet (2000); 8: Barthelt *et al.* (1991); 9: Ledoux (1972); 10: Cappetta (unpubl.); 11: Cigala Fulgosi (1986); 12: Aguilera and Rodrigues de Aguilera (2001). [Registre fossile des genres d'Etmopteridae. Les cartouches noirs et gris indiquent respectivement les présences certaines et probables de taxa d'Etmopteridae. La diversité en nombre d'espèces est représentée par la quantité de carrés unitaires. Les références bibliographiques sont indiquées près de chacun des cartouches. 1 : Underwood et Mitchell (1999) ; 2 et 3 : voir Siverson (1993), Siverson et Cappetta (2001) ; 4 : Siverson (1993), Thies et Müller (1993) ; 5 : modifié d'après Welton et Farish (1993) ; 6 : Cappetta et Adnet (2001) ; 7 : Adnet (2000) ; 8 : Barthelt *et al.* (1991) ; 9 : Ledoux (1972) ; 10 : Cappetta (non publié) ; 11 : Cigala Fulgosi (1986) ; 12 : Aguilera et Rodrigues de Aguilera (2001).]

Ledoux (1972) was correct to place “rather arbitrary these teeth in the genus *Centroscyllium*” [“assez arbitrairement ces dents dans le genre *Centroscyllium*”] (p. 156); while he could not know the recent genus *Miroscyllium*, which was not known at that time. Contrary to Casier’s (1961) opinion, Ledoux considered this dental morphology as the passage to the modern type *Centroscyllium* with multicuspidate lower teeth from a primitive stage of *Etmopterus* type. Siverson (1993) agrees partially with this opinion and considers the dentition of *Centroscyllium* to be the result of a brutal and instantaneous change from the upper dentition of *Etmopterus*.

The present paleontological data do not allow to solve all phyletic conflicts within Etmopteridae, because of the evolution from the mono- to multicuspidate crown. Recent phylogenetical analyses place *Centroscyllium* at the base or as the sister group of *Etmopterus*/*Miroscyllium* (Shirai and Nakaya, 1990b; Shirai, 1992; Carvalho and Maisey, 1996). The absence (in the present state of knowledge) of fossil representatives of the *Centroscyllium*/*Aculeola*-group and the very early occurrence of the *Etmopterus*/*Miroscyllium*-group in the fossil record are indeed incompatible with the last hypotheses.

According to Siverson (1993), the absence in the fossil record could be due to inadequate sampling of Cenozoic deep-water and small-sized elasmobranchs. The lack of those genera on the long list of Squaliformes occurring at the Middle Eocene of Landes (Adnet, 2000) indicates that the reason of their absence might be more complex and certainly related to their evolutionary history.

CONCLUSION

This study contributes to the knowledge about the dentition of the extant Etmopteridae genus *Miroscyllium*. It confirms the strong ontogenetic heterodonty, with juvenile specimens showing a dentition very different from adult dentitions. It is proposed here that *Miroscyllium* represents the link between *Etmopterus* and *Centroscyllium*.

Fossil *Miroscyllium* species share numerous characters with lower teeth of *Etmopterus* such as a rectangular-shaped root, strong labiolingual compression, many well-developed overlapping root surfaces, very flat labial face of the root, lingual face of the root being reduced to the transverse bulge, and the presence of one mediobasal foramen. As in the living species *M. sheikoi*, lower teeth of fossil species can be separated from those of *Etmopterus* species by a multicuspidate crown in the adult stage. However, lower fossil teeth appear to be less derived than those in *M. sheikoi*. In fact,

fossil lower teeth show a cusp which is slender towards the rear with a concave profile of the mesial cutting edge, a well-marked transversal bulge and some well-developed overlapping surfaces.

The Miocene species from southern France seems to be less derived than the living species of *Miroscyllium* but largely more derived than *Etmopterus* species, based on its dentition. Contrary to the interpretation of Casier (1961), while the genus *Miroscyllium* was not yet described, Ledoux (1972) considered the peculiar dental morphology of the fossil species to represent the link between derived morphology of *Centroscyllium* (multicuspidate lower teeth) and the least derived morphology of *Etmopterus* (monocuspidate lower teeth). Independently, Siverson (1993) partly agreed with this point of view and while adequate illustrations of *Miroscyllium* were not available, considered that the modern *Centroscyllium* dentition resulted from a “brutal and instantaneous” genetic change from the upper dentition of *Etmopterus*.

The new figures of *Miroscyllium* dentition lead to the conclusion that the evolutionary interpretation of Ledoux (1972) as realistic. Moreover, the early occurrence of *Etmopterus* and *Miroscyllium* in the fossil record (Fig. 4) compared to the present lack of fossils of *Centroscyllium* and *Aculeola* supports this interpretation. However, this hypothesis based on the transition from the mono- to multicuspidate lower teeth is inconsistent with recent results of phylogenetic analyses, which place the *Centroscyllium*/*Aculeola*-group as less derived than the *Etmopterus*/*Miroscyllium*-group (Shirai and Nakaya, 1990b; Shirai, 1992; Carvalho and Maisey, 1996). As Siverson (1993) remarks, lack of some Squaliformes in the fossil record could be explained by the scarcity and the difficulties of collecting deep-water fossil elasmobranchs. However, the lack of *Centroscyllium* and *Aculeola* ancestors from the long list of fossil Squaliformes in a new and rich fossiliferous excavation in Angoumé (southern France, Adnet 2000) supports our point of view. The absence of their fossil representatives seems to be more complex and is certainly related to their life-history. Only new phylogenetic and paleontological studies will lead to a better understanding of the evolution of these peculiar small and deep-water lantern sharks.

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